

A REVISION OF THE NORTH AMERICAN GENUS UVULARIA (LILIACEAE)

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The endemic North American genus *Uvularia* is comprised of five species with one or more of these being frequently encountered from Nova Scotia south into northern Florida and west into Louisiana and eastern North Dakota. All of the species are very attractive members of the early spring flora and hence are widely known and often collected.

As is befitting a small and uncomplicated genus, its history is a simple one. It was founded by Linnaeus in 1738 in his *Hortus Cliffortianus* but takes 1753 as its starting point for nomenclatural purposes. Linnaeus recognized three different species (*U. amplexifolia*, *U. perfoliata* and *U. sessilifolia*) of which only the second and third species, which possess capsular fruit, are now considered to belong to that genus, or by some to it and a closely related segregate. Linnaeus' *U. amplexifolia*, whose fruit is a berry, has been treated as a member of the genus *Streptopus* since the early nineteenth century. As is demonstrated by the extensive list of "excluded names" at the end of this paper, earlier botanists had a much broader concept of the genus which included members of the following genera: *Disporum* (including *Prosartes*), *Fritillaria*, *Streptopus* and *Tricyrtis*. However, at least by the last quarter of the nineteenth century, these extraneous elements had been removed and the

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genus (or the group of two closely related genera) was restricted to the same eastern North American species that we recognize today.

Watson (Proc. Am. Acad. 14:221, 268, 269. 1879) segregated the two sessile-leaved species recognized by him from the perfoliate species, naming the first mentioned group *Oakesia*. In reviewing this paper, Asa Gray (Am. Jour. Sci. ser. 3. 18: 314. 1879) expressed his disinclination to accept the segregate although admitting the several "good" differences upon which the separation was based. The genus was taken up, however, in the sixth edition of Gray's Manual which Watson co-edited with Coulter. The segregate was also recognized by Small who, however, provided the substitute name *Oakesiella* since, under the American Code, which he more or less followed (as under the more recent versions of the International Code), a later homonym could not be employed even if the first use of the name were treated as a synonym. In addition to Gray, mentioned above, the segregate has been rejected by Bentham and Hooker (Gen. Pl. 3:830. 1833), Engler (Nat. Pflanzf. II. 5: 24. 1888), Britton (Bull. Torrey Club 18: 272. 1891), Fernald (Gray's Man. 8th ed. P. 428, 429. 1950), and Gleason Ill. Fl. 1:428. 1952), while *Oakesia* or *Oakesiella* has been taken up by Small (Fl. Se. U. S. 271, 272. 1903; Man. Se. Fl. 299, 300. 1933), Robinson and Fernald (Gray's Man. 7th ed. p. 280, 285, 286. 1907), Macbride (Contr. Gray Herb. 53:5. 1918) and Rydberg (Fl. Plains & Prairies p. 219, 221, 222. 1932).

INTERGENERIC RELATIONSHIPS

Unfortunately, it is not possible to discuss meaningfully the generic affinities of *Uvularia*. The tribe Uvularieae has been variously interpreted since it was first published by Kunth (Enum. Pl. 4: 199-214. 1843). In addition to *Uvularia* it then included such American genera as *Streptopus* Michx. (including *Hekorima* Raf.), *Disporum* Salisb. (including *Prosartes* Don), and four other genera from the Old World. There is a high degree of correspondence as to the contents of the tribe in the works of Bentham and Hooker

(Gen. Pl. 3:829-832. 1883), Engler (Nat. Pflanz. II. 5: 24-27. 1888) and Hutchinson (Fam. Fl. Pl. 2:606. 1959). The last two authors however, restrict the tribe to capsuled genera, thus excluding the baccate *Disporum* which was relegated by both of them to the tribe Polygonateae. None of the other genera included in the tribe by Hutchinson possesses a range that is ordinarily to be expected for very close relatives of eastern North American plants. Engler placed the eight genera of his concept in his Melanthioideae — Uvularieae all of which, with the exception of *Uvularia*, are confined to the Old World continents of Africa, Asia and Australia. Only one of the Asian genera, the aberrant, septicidally dehiscent *Tricyrtis* (considered by Hutchinson as the type of another small, ditypic tribe), reportedly from Japan, Korea, China and the Himalayas, possesses a range that is an expected one for close relatives of eastern North American plants. Until considerably more knowledge is acquired, the classifications of the Liliaceae, like most large taxa, will continue to be artificial, being largely based upon one or very few characters, and hence speculation as to the generic relatives of a genus such as *Uvularia* will remain most unproductive and unconvincing.

MORPHOLOGY

HABIT. All five species are perennial herbs whose aerial parts die back to the ground each winter.

UNDERGROUND PARTS. The five species are divisible into two distinct groups upon the basis of their underground parts. Three species possess a very short (less than 1 cm long) underground rhizome from which arise the annual aerial stems and from which descend a cluster of thickened roots. One of these species (*U. perfoliata*) spreads by means of a pair of slender, subterranean stolons, each of which forms buds and roots at its distal end, after which the connecting portion of the stolon disintegrates. These structures have been seldom observed but this is not surprising as considerable care must be devoted in securing them intact. Whether they are present or absent in the other two species (*U. grandiflora* and *U. puberula*) with a similar rhizome

and root system is at present unknown but they have at least not been observed. Two species (*U. sessilifolia* and *U. floridana*) possess elongate (10 cm long or more), thickened rhizomes from which descend scattered fibrous roots and from the tips of which ascend the aerial stems.

AERIAL STEMS. In all species flowering or fruiting stems appear to be once-branched if one ignores the short, flowering or fruiting branches. The branching pattern is sympodial. The stems of the perfoliate species are terete and hollow while those of the sessile-leaved group are typically strongly angled (at least above) and solid.

LEAVES. The genus is divisible into two distinct groups based upon whether the leaves are perfoliate or sessile. (The two groups however are not the same as would result from a division based upon the subterranean parts.) The upper leaves of the perfoliate group are merely sessile and strongly clasping or amplexicaul. The leaf margins of the perfoliate-leaved species are perfectly smooth while those of the sessile-leaved species are all very minutely papillose.

INFLORESCENCE. The flowers are solitary and terminal although superficially appearing lateral or axillary and often so described (*e. g.* Dietz, p. 221). The pattern of growth is hence sympodial. The flowers of *U. floridana*, *U. perfoliata*, and *U. grandiflora* are borne on short branches bearing a small to large leaf (= bract) at the base of the pedicel. This feature has been rarely seen on specimens of *U. puberula* and it has never been observed in *U. sessilifolia*. It would be of considerable interest to know if there is any anatomical evidence as to whether those species lacking the flower-or fruit-subtending bract have merely lost the bract or have lost both bract and the supporting stem.

INDUMENT. *Uvularia perfoliata*, *U. floridana* and *U. sessilifolia* are completely glabrous. The lower leaf-surface of *U. grandiflora* is usually densely short-pubescent but the degree of pubescence varies from dense to almost, or rarely even completely, glabrous. Dietz (1952) has concluded that this variation is due to introgression from *U. grandiflora* into the glabrous *U. perfoliata* but, as areas of comparative

glabrousness of what surely is *U. grandiflora* are to be found in Arkansas and Minnesota far from the influence of *U. perfoliata*, it would seem that another or an additional explanation is required. *Uvularia puberula* is exceedingly variable as to the presence and amount of pubescence, its distribution and even the length of the trichomes. The pubescence is usually to be found, when present, upon the angles of the upper portion of the stem but sometimes extends onto the lower surface of the leaves along the elevated principal veins. In some specimens of this species no pubescence is to be detected and this feature is characteristic of the so-called var. *nitida*.

PERIANTH. The perianth is a typically liliaceous one consisting of 6 distinct tepals arranged in two imbricate series. The tepals of *U. perfoliata* are the most distinctive in the genus because of the presence of granular papillosities on their inner surface. There is a tendency for the size and shape of the tepals to be more or less characteristic of each species but the variation is so great that the tendencies are not too helpful. The tepals are rendered somewhat gibbous at base through the presence of a nectariferous pouch at the base of each perianth-segment. Small (1903, 1933) was in error in stating that the sessile-leaved species (*Oakesiella*) lack nectaries. Watson (1879) stated that the perfoliate species were characterized by the presence of a callus or ridge on either side of the nectary while the sessile-leaved group lacked the ridge. Study of pickled flowers of all five species indicated that a moderately to slightly elevated, thin flap was present on each side of the nectariferous depression in the two perfoliate-leaved species while only the slightly hardened wall of the nectary was present in the sessile-leaved species. This distinction is however, difficult to detect and hence of little taxonomic utility.

STAMENS. The six stamens usually have been described as adnate to the very base of the tepals and this may be their actual condition but they appear to me to be attached to the receptacle slightly above the tepals. The slightly flattened filaments are about half-again as long (or even less) as the

linear, laterally dehiscent, extrorse, adnate anthers. The stamens appear to be of slightly different lengths in two alternating series but this is the result of the slight difference in attachment levels of the two series. The connective extends beyond the anther-sacs in all the species but is most obviously exerted in *U. perfoliata*. The degree of exertion is quite variable.

PISTIL. The ovary is sessile or very nearly so in all species but *U. sessilifolia*, which possesses a stipitate ovary. The stipe appears to be merely the sterile base of the ovary. The ovary is in general rounded (although lobed) in the two perfoliate-leaved species but sharply angled in the three sessile-leaved species. The stigma is moderately to deeply cleft in the various species, being probably most deeply divided in *U. puberula* and *U. grandiflora* and the least so in *U. floridana* and *U. sessilifolia*. Fernald (*Rhodora* 37: 409. 1935) reported that *U. puberula* exhibits heterostyly (which, if true, would be a most unusual condition in the Liliaceae) but it appears from admittedly casual observations that the variation in length of style and exertion of the stigmatic branches beyond the anthers within a given species is almost completely a matter of age. The flowers are apparently protandrous.

FRUIT. The loculicidally and tardily dehiscent capsules offer a ready means of identification but the distinguishing features are often lost in pressed specimens. The fruits of the perfoliate-leaved species are more or less truncate at the apex while those of the sessile-leaved species gradually taper to an acute (*U. puberula* and *U. sessilifolia*) or even to a long-beaked apex (*U. floridana*). The fruit of *U. perfoliata* is more or less angularly obpyramidal and each of the three lobes is deeply bifid, thus appearing 6-horned. The fruit of *U. grandiflora* is more roundedly obpyramidal and with very little or no evidence of deeply bifid or 2-horned angles. The fruits of the sessile-leaved species are much more sharply angled, with *U. sessilifolia* being at once distinguished by its long-stipitate base in contrast to the sessile or very nearly sessile bases of the other two species.

The long-rostrate beak of *U. floridana* distinguishes that species from *U. puberula* as well as all other species in the genus.

SEEDS. The seeds of the perfoliate-leaved species, which possess an apparent outgrowth of the raphe which at first is a swollen, balloon-like sac but at maturity deflates into a thin membrane nearly half-enveloping the seed, are at once distinguishable from the two turgid ridges which parallel the raphial slit in the seeds of the three sessile-leaved species. The nature of these outgrowths is unfortunately unknown.

ANATOMY

Holm (Bull. Torrey Club 18: 1-5. 1891) presented the only account known to me concerned with the internal anatomy of any species of this genus. He compared the anatomy of two species: *U. perfoliata* and *U. sessilifolia*. The results of his anatomical comparison are presented in the chart below.

	<i>U. sessilifolia</i>	<i>U. perfoliata</i>
1. Walls of endodermis	Thin	Thick
2. Number of fibro-vascular bundles in root	20	10
3. Number of layers of cells between epidermis of stem and mechanical tissue	1	2
4. Number of layers in mechanical tissue of stem	5	2

Eames (Chronica Bot. 14: 128, 129. 1953), although presenting no supporting evidence, made the following statement: "Anatomically there is no basis for the maintenance of *Oakesia*. There is more anatomical difference between *U. perfoliata* and *U. grandiflora* than between *U. grandiflora* and *Oakesia*." It is to be hoped that the evidence for such a sweeping statement will soon be presented, for it is difficult to conceive of anatomical evidence that would show a closer relationship of *U. perfoliata* to a species such as *U. sessilifolia* than to *U. grandiflora*.

Anderson and Hubricht (Am. Nat. 77: 285-287. 1943), by making celloidin peels of herbarium specimens, found that the "epidermal cells of *Uvularia grandiflora* tend to be larger, more irregular and more variable than those of *U. perfoliata*" and concluded that this tendency resulted in "a coarser, cruder leaf-texture".

CYTOLOGY

Anderson and Whitaker (1934) reported the chromosome number for three species (*U. grandiflora*, *U. perfoliata* and *U. sessilifolia*) to be $n = 7$. The chromosomes were found to be large, and each was identifiable by its distinctive morphology. They concluded from this study that "there is no evidence that chromosome duplication or chromosome interchange are of phylogenetic importance in *Uvularia*." Previously Belling (Jour. Genetics 15: 245-266. 1925) demonstrated in *U. grandiflora* that under experimental conditions non-disjunction, fragmentation, lack of pairing and duplication of all or part of the chromosome complement all occur.

Belling also reported that meiosis of the pollen mother cells in his plants of *U. grandiflora* grown in a cool greenhouse took place in late February. Alden (Bull. Torrey Club 39: 439-446. 1907) reported for *U. sessilifolia* that mature microspore mother cells are to be found by the middle of September and that these divide by October and overwinter as microspores. Meiosis within the ovule however did not occur prior to late April and even the megaspore mother cells were not formed prior to mid-March.

Sato (Jap. Jour. Bot. 12: 76. 1942) reported that the *U. sessilifolia* studied by him (apparently grown from botanical garden material) had $2n = 16$ and not $2n = 14$ as indicated by Anderson and Whitaker. The reason for this discrepancy has not been determined. Since the chromosome number of several Japanese species of *Disporum* including *D. sessile* (= *Uvularia sessilis*) is $2n = 16$, suspicion is aroused as to the identity of Sato's material.

INTRAGENERIC RELATIONSHIPS

A suggestion as to the probable relationships between the

species is presented in the accompanying figure (fig. 1). Such a hypothetical scheme is of course highly subjective and hence open to criticism but for most taxa of plants we now have little choice but to attempt to visualize a hypothetical ancestral type from which a suggested "phylogeny" for the group may be logically derived.

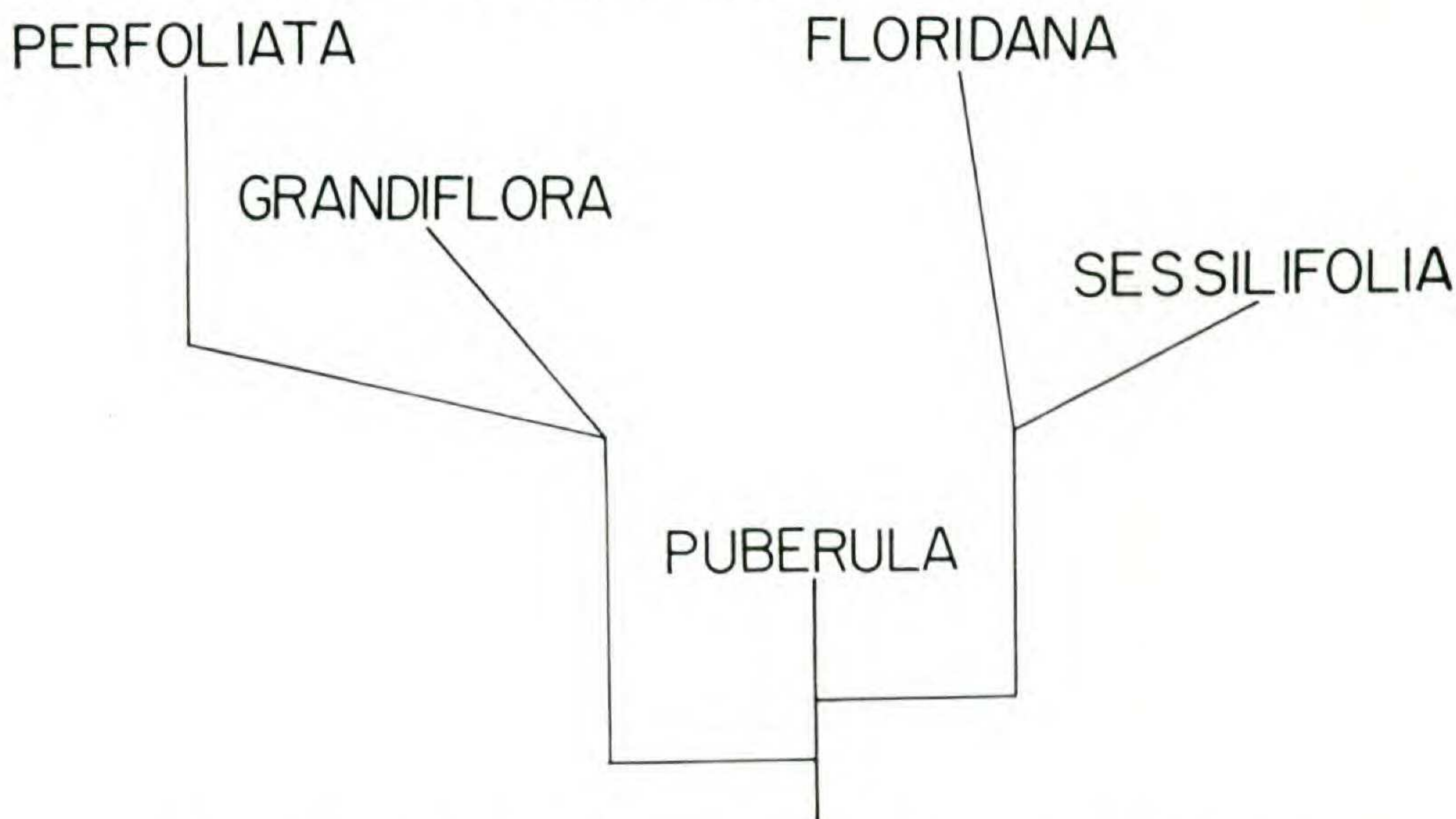


Fig. 1. Probable relationships of the species of *Uvularia*

An attempted reconstruction of the more immediate hypothetical ancestral taxa of these five species of *Uvularia* would result in a perhaps pubescent perennial with a very short rhizome or caudex, fleshy roots, sessile leaves and sympodially arranged flowers borne on a leafy-bracted short branch. This plant would most closely resemble *U. puberula* which, however, only very rarely possesses a leafy bract.

There would seem to be no doubt that sessile leaves are more primitive than perfoliate ones. (The presence of sessile leaves at the ends of the branches and the increasing perfoliateness of leaves are thought to be evidence of this.) There is certainly much less evidence that a very short rhizome is more primitive than an elongate rhizome or that the presence of pubescence is a primitive characteristic and its absence an indication of evolutionary advancement. But both of these assumptions are here made since the short-rhizomed, puberulent, sessile-leaved species, *U. puberula*,

resembles the two perfoliate-leaved species in its underground parts. With its similar unornamented tepals, *U. puberula* is seemingly more closely related to the puberulent *U. grandiflora* than to the apparently more specialized papillate-tepaled *U. perfoliata*. The presence of leafy bracts below the flowers or fruits of *U. floridana*, *U. grandiflora* and *U. perfoliata* is here interpreted to be a primitive character. Those species lacking this bract are thought to have lost it through suppression. Several specimens of otherwise unmistakable *U. puberula*, but with a small subtending bract, were noted in this study. (It would be, however, of considerable interest to know if there is any anatomical evidence of the hypothesized suppressed leafy bract within the two species.) And finally the stalked fruit of *U. sessilifolia* is thought to be an indication of advancement.

SUBGENERIC CLASSIFICATION

Evaluation of the taxonomic merit of such a segregate as *Oakesiella* (= *Oakesia*) is of course highly subjective. The two groups give every morphological evidence of being natural and yet whether the two taxa are better accorded generic or subgeneric rank is largely a matter of individual taste. It is believed however that criteria suggested by McVaugh (*Wrightia* 1: 15, 16. 1945) for the evaluation of proposed generic segregates are met with by *Oakesiella*. I choose to recognize the two taxa as well-defined sections but others with whom I could not argue no doubt would consider that the differences warranted subgeneric status and still others would deem the degree of divergence represented as meriting no more than the rank of series. And of course many would perhaps rightly consider it folly to erect a formal subgeneric classification within so small and relatively homogeneous a taxon.

SYSTEMATIC TREATMENT

Uvularia L., Sp. Pl. 304. 1753; Gen. Pl. 144. 1754.

Anonymos Walt., Fl. Car. 122. 1788. *nom. illegit.* Art. 20. *Oakesia* S. Wats., Proc. Am. Acad. 14:221. 1879; not *Oakesia* Tuckerm., Hook. Lond. Jour. Bot. 1: 445. 1842 which = *Corema* G. Don, Edinb.

New Phil. Jour. 2: 63. 1826. *Oakesiella* Small, Fl. Se. U. S. 271, 1328. 1903.

Pubescent or glabrous, occasionally glaucous, perennial herbs with very short or elongate rhizomes and with thickened or fibrous roots. Stems erect, terete to strongly angled, and, excluding the flowers, but once branched, with several sheathing, papery cataphylls below the blade-bearing leaves. Branching-pattern sympodial. Leaves alternate, perfoliate or sessile, oblong-linear to oblong-ovate and longitudinally several- to many-nerved. Flowers solitary, terminal but appearing axillary, pendant, narrowly campanulate. Perianth 6-parted; the segments multiveined, similar to one another in two imbricate series, distinct, pale- to deep-yellow, linear-oblong, obtuse to acute, slightly gibbose at base with a nectariferous depression, dropping off along with the stamens several days after pollination. Stamens 6, hypogynous, apparently completely free from the tepals, always shorter than the perianth segments; filaments slightly flattened and dilated below, rather short, being several times exceeded in length by the pollen sacs; usually noticeably but slightly alternating with one another in length with 3 longer and 3 shorter; anthers elongate, linear-oblong, extrorse, adnate, dehiscing by a longitudinal slit down the abaxial face; connective slightly to conspicuously exserted, its apex acute to obtuse or even truncate. Pistil 3-carpellate; ovary 3-loculate, sessile to conspicuously stipitate, rounded- to sharply-triangular in cross-section, truncate to acute or even rostrate at apex, acutely tapering at the base; style united for about one-third to two-thirds the distance from ovary to the tip of the tripartite stigma, deciduous at maturity; stigmas linear, at first appressed together but arching outward at maturity and stigmatic along inner surface. The style and stigmatic lobes at first exceeded in length by the anthers but later exceeding them. Ovules anatropous, 2-6 per locule, horizontal from axile placentae. Fruit a greenish to stramineous (or in age becoming brownish) loculicidal capsule with walls smooth or pebbled within. Seeds globose, smooth, few (1-3) in each locule at maturity, with a very small embryo and a hard, white endosperm.

LECTOTYPE: *Uvularia perfoliata* L. (First chosen by Britton and Brown, Ill. Fl. ed. 2. 2: 518. 1913, but indirectly determined by Watson's exclusion of *U. sessilifolia* in 1879.)

KEY TO THE SECTIONS OF UVULARIA

Leaves sessile, their margins scarious but also very minutely papillose-denticulate; seeds with a thick ridge-like crest bordering each side of the slit-like raphe; capsule acute at apex; the inner surface of fruit smooth or at least not densely pebbled. .. Section 1. OAKESIELLA.
Leaves perfoliate, their margins scarious but smooth; seeds largely surrounded by a bladdery sac, this later becoming a flattened, membranous, loose envelope nearly half-enclosing the seed; capsule trun-

cate at apex or at least not gradually tapering from near the middle; inner surface of fruit densely pebbled. Section 2. UVULARIA.

Section 1. OAKESIELLA (Small) stat. nov.

Oakesia S. Wats., Proc. Am. Acad. 14: 269. 1879; not *Oakesia* Tuckerm., Hook. Lond. Jour. Bot. 1: 449. 1842 = *Corema* G. Don, Edinb. New Phil. Jour. 2: 63. 1826. *Oakesiella* Small, Fl. SE. U. S. 271, 1328. 1903.

Pubescent or glabrous herbs with elongate or very short rhizomes and with either scattered fibrous or clustered, thickened, fleshy roots. Stems triquetrous, at least above. Leaves sessile and, if sometimes appearing somewhat clasping at base, never perfoliate, margins minutely denticulate. Ovary conspicuously 3-angled in cross-section and tapering from middle to both apex and base. Capsule acute at apex; the inner surface of fruit smooth or slightly ridged but never densely pebbled. Seeds with two swollen, elevated ridges paralleling the raphial slit.

LECTOTYPE: *Oakesiella sessilifolia* (L.) Small = *Uvularia sessilifolia* L. (Chosen by Small, Fl. Se. U. S. 1328. 1903).

KEY TO THE SPECIES OF THE SECTION OAKESIELLA

1. Stigmatic lobes nearly equaling or at least not more than twice exceeded by the undivided style; upper stems and sometimes the lower surfaces of the leaves often moderately to densely puberulent but occasionally glabrous; aerial stem arising from a very short rhizome (less than 0.5 cm. long) with clustered, thickened roots 1. *U. puberula*.
1. Stigmatic lobes 3-5 times exceeded by the length of the undivided style; stem and lower surfaces of the leaves always glabrous; aerial stem arising from an elongate fleshy rhizome with scattered fibrous roots.
 2. Short flowering-branchlet bearing a foliaceous bract stigmatic lobes 3 mm. long or longer; capsule sessile at base and conspicuously rostrate at apex; connective of filament exerted 0.5 mm. or more beyond anther-sacs; tepals with an acuminate apex 2. *U. floridana*.
 2. Short flowering-branchlet lacking a bract; stigmatic lobes less than 3 mm. long; capsule clearly stipitate and lacking a rostrate beak; connective of filament barely, if at all, exerted beyond anther-sacs; tepals rounded to acute at apex 3. *U. sessilifolia*.

Section 2. UVULARIA.

Pubescent or glabrous herbs with very short rhizomes and with clustered, thickened, fleshy roots. Stem terete. Leaves perfoliate (except for the uppermost which is merely sessile); margins smooth. Ovary rounded in cross-section although usually with 3 principal lobes.

and each of these bilobed to a lesser extent. Capsule truncate at apex; the inner surface of fruit densely pebbled. Seeds first partly enveloped by a large, swollen, balloon-like sac which at maturity becomes deflated and then forms a membrane which half envelopes them.

KEY TO THE SPECIES OF SECTION UVULARIA

- Perianth-segments glabrous within; leaves usually at least moderately puberulent beneath but rarely glabrate; connective of filament extended less than 0.8 mm. beyond anther-sacs; principal capsule-lobes neither deeply lobed nor 2-horned; blade-bearing leaves below the lowest branch typically but one 4. *U. grandiflora*.
- Perianth-segments conspicuously granular-papillate within; leaves glabrous beneath; connective of filament extended more than 0.8 mm. beyond anther-sacs; principle capsule-lobes deeply 2-lobed or 2-horned; blade-bearing leaves below the lowest branch typically 3-4 5. *U. perfoliata*.
1. **Uvularia puberula** Michx., Fl. Bor.-Am. 1: 199. 1803. (Type presumably at Paris, but not seen. Description is such that no other species could have been meant.) *Oakesia puberula* (Michx.) S. Wats., Proc. Am. Acad. 14: 269. 1879. *Oakesia sessilifolia* var. (?) *nitida* Britt., Trans. N. Y. Acad. Sci. 9: 13. 1899. (Type! NY, Isotypes GH, CHRB.) *U. sessilifolia* var. *nitida* (Britt.) Morong, Mem. Torrey Club 5: 111. 1894. *U. nitida* (Britt.) Mackenzie, Torreyana 8: 14. 1908. *Oakesiella puberula* (Michx.) Small, Fl. Se. U. S. 272, 1328. 1903. *Oakesiella nitida* (Britt.) A. A. Heller, Muhlenbergia 6: 83. 1910. *U. puberula* var. *nitida* (Britt.) Fern., Rhodora 37: 407. 1935. *U. pudica* var. *nitida* (Britt.) Fern., Rhodora 41: 536. 1939.

Plant usually moderately to densely short-puberulent on the upper portion of the stem, especially at the nodes and occasionally sparingly so on the lower surface of the leaves but rarely glabrous or very nearly so throughout; the stem conspicuously angled above and often triquetrous, about (2.0-) 2.5-4.5 (-5.0) dm. tall with several stems arising in a cluster from a very short rhizome and with a cluster of descending fleshy roots. Leaves dark green above and lighter green beneath, glabrous or very sparingly short-puberulent below, especially near the base of the principal veins, mostly (3.5-) 4.5-7.5 (-8.5) cm. long and (1.0-) 1.7-3.2 (-4.0) cm. wide, oblong-elliptic to broadly elliptic in general outline with a broadly rounded, sessile to subclasping base, and an acute to even abruptly short-acuminate apex; the leaf subtending the first branch about (3.7-) 4.5-6.5 (-8.0) cm. long and (0.9-) 1.0-2.0 (-2.5) cm. wide. Blade-bearing leaves below the first branch typically but one. Leaf-margin very minutely but abundantly papillose-denticulate and very slightly scariously edged. Flower borne solitary and terminating the stem but appearing as if lateral and borne opposite the leaf; its downwardly arching peduncle lacking a leaf or bract and in flower

about 0.5-1.4 (-2.0) cm. long and glabrous to densely short-puberulent. Perianth segments about (1.0-) 1.5-2.5 (-2.7) cm. long and (1.5-) 2.0-4.0 (-5.0) mm. wide; each tepal more or less tapering to a rounded apex. Tepals fleshy-thickened for about the basal 1-1.5 mm. with an indistinct, shallow, wedge-shaped, nectariferous depression about 1 mm. long and 0.5-0.8 (-1.2) mm. wide; the nectary scarcely bordered on either side by a short ridge that is but little elevated above the surface of the tepal. Filaments smooth, oblong to linear and scarcely if at all tapering from middle to either apex or base, about (1.5-) 2.0-4.0 (-5.5) mm. long and about 0.8-1.2 mm. wide. Connective extending beyond the anther-sacs for about 0.6-0.8 mm. and about 0.5 mm. wide, very slightly inwardly arching and very conspicuously truncate. Anther-sacs about (5.0-) 7.0-12.0 (-13.0) mm. long. Ovary conspicuously triquetrous (except through abortion of one locule), tapering distinctly to both apex and base, hence appearing shortly stipitate; the three sides of the ovary appearing slightly concave but not at all medially lined or grooved, about 0.5-0.8 cm. high and each face about 2.5-3.5 mm. wide. Style united for about one-half the distance to the stigmatic tips which somewhat reflex with age; style and stigmas together about 8.0-14.0 mm. long. Capsule typically conspicuously three-winged, triquetrous and roundedly tapering to both apex and base, its sides somewhat concave and each face appearing broadly elliptic in outline; its base scarcely stalked (at most 1-1.5 mm.); about (1.5-) 1.8-2.7 (-3.5) cm. long and (1.0-) 1.5-2.0 (-2.2) cm. wide, dotted reddish-brown. Seed globose or nearly so, about 3.0-5.0 mm. in diameter, reddish-brown at full maturity but straw-colored when it first reaches full-size and with a thickened mound-like crest extending along either side of the slit-like raphe and about half encircling the seed. Usually in moist but well-drained wooded sites from New York (Long Island) and New Jersey, then in the Coastal Plain and lower Piedmont of southeastern Virginia south into Georgia and in the mountains and upper Piedmont from southern Pennsylvania south to west-central Georgia (Fig. 2).

There is considerable variation in the amount of pubescence exhibited by individual plants of this species, ranging from glabrous to very densely puberulent. The representatives of the species found in New Jersey are apparently all of the glabrous type, but elsewhere within the range of the species equally glabrous plants are to be found. And even more frequently encountered are individuals that are only moderately to sparsely puberulent. The glabrous tendency has been treated as a variety by Britton, Morong, and Fernald and as a species by Mackenzie. Fernald stressed, in addition to the glabrousness of this taxon, its thinner and

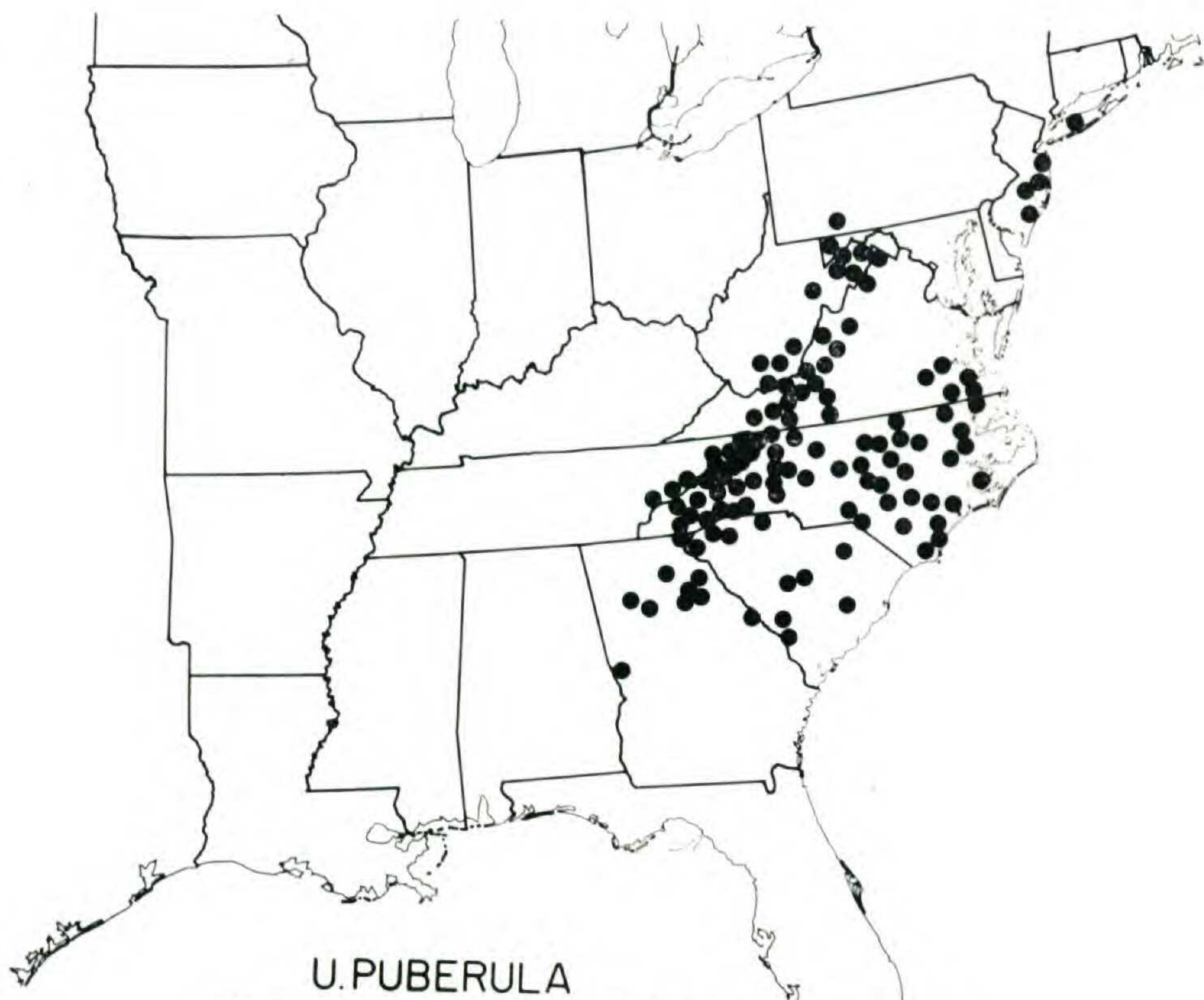


Fig. 2. Distribution of *Uvularia puberula*

less prominently reticulate leaves and gave its range as Long Island, New Jersey and southeastern Virginia. I have found equally glabrous plants (often included on the same sheet as densely puberulent ones) in the mountains of Virginia, West Virginia and the Carolinas but have not considered that the variation warranted formal taxonomic recognition. Although glabrous plants are more frequent in the Coastal Plain, puberulent individuals are also encountered there. Recognition of a glabrous variety largely restricted to the Coastal Plain would appear somewhat more plausible if the individuals were either glabrous or densely puberulent instead of ranging fully between the two extremes.

The vegetative parts of this species are thicker and more sturdy than those of any other species and its leaves and fruit persist in a green and apparently vigorous condition until frost or for several months later than its congeners.

As discussed in the section on "Dubious and Excluded Names", I now believe that I was too hasty in proposing a

new combination, based upon Gmelin's *Erythronium carolinianum*, as the proper name of this species.

2. *Uvularia floridana* Chapm., Fl. S. U. S. 487. 1860. (Type not seen. Original description thought to be conclusive.) *Oakesia floridana* (Chapm.) Macbride, Contr. Gray Herb. n.s. 53: 5. 1918. *Oakesiella floridana* (Chapm.) Small, Fl. Se. U. S. 272, 1328. 1903.

Plants completely glabrous and the upper stem and lower surfaces of the leaves slightly glaucous; the stem about 2.5-4.0 (-4.5) dm. high and triquetrous at least above and arising from a branching, whitish, fleshy rhizome about 3-5 mm. in diameter. Leaves glabrous, narrowly to broadly elliptic with a tapering to rounded base and an acute to rounded apex, mostly 4.0-7.0 (-8.5) cm. long and (1.2-) 1.8-3.0 cm. wide; the leaf subtending the lowest branch mostly about 4.0-7.5 cm. long and 1.2-2.8 cm. wide. Blade-bearing leaves below the lowest branch 1-2. Leaf-margin scarious and very minutely but densely denticulate. Fertile branchlet composed of a strongly 3-angled, slightly hyaline-winged stem about (0.8-) 1.2-1.6 (-2.0) cm. long; an ovate to lanceolate foliaceous bract with a rounded base and an acute apex mostly 1.0-2.0 (-3.0) cm. long, and a terete peduncle about 2-8 mm. long and

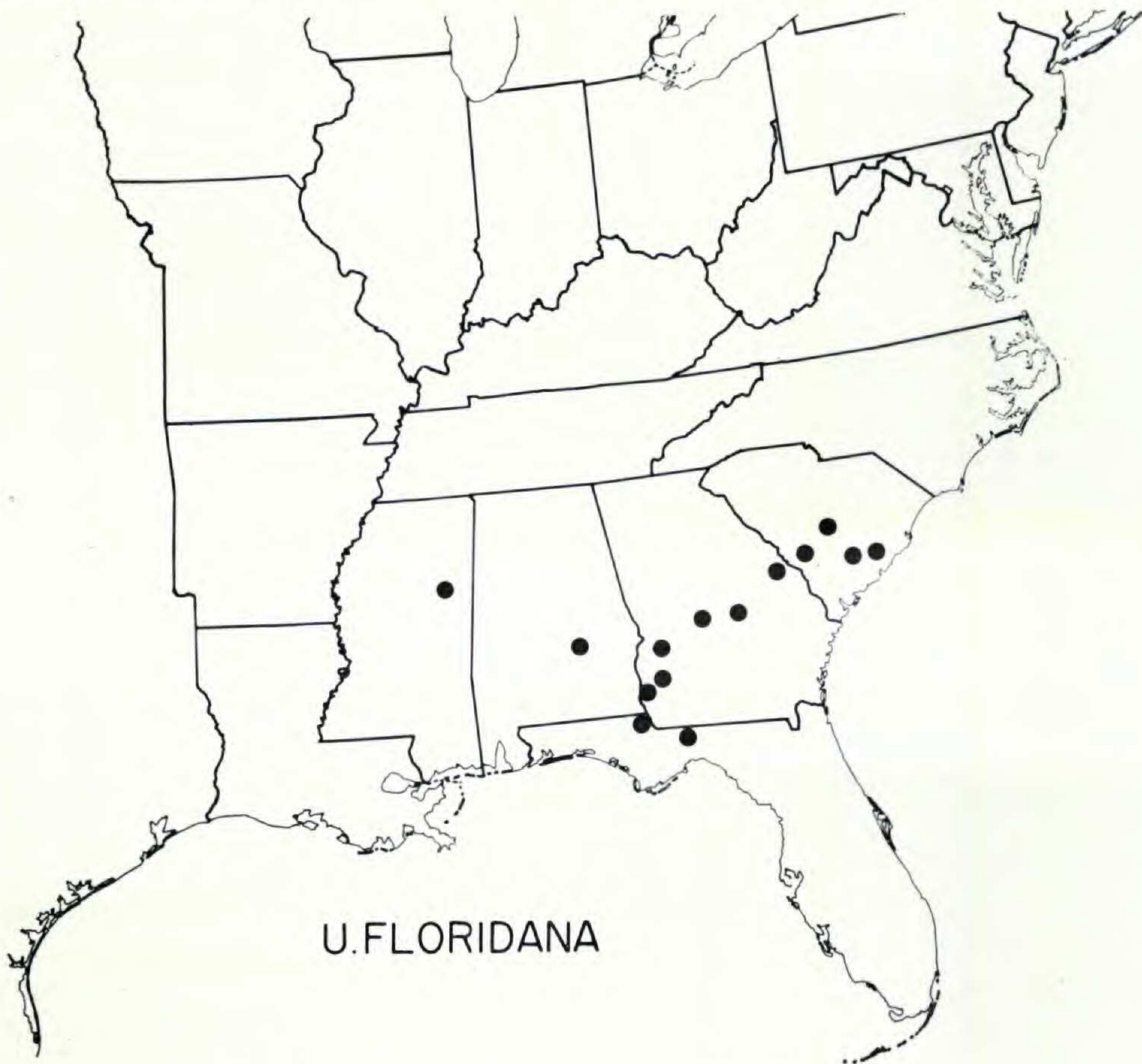


Fig. 3. Distribution of *Uvularia floridana*

one flower. Perianth-segments about (1.8-) 2.2-3.0 cm. long and about 3-4 mm. wide, tapering to an acuminate apex, perfectly smooth both internally and externally, very pale yellowish-white. Tepals narrowing basally into a thickened, somewhat fleshy, channeled base about 1.0-1.8 mm. long with a well-defined, narrow, nectariferous depression about 0.8-1.4 mm. long and 0.5-1.0 mm. wide with more or less parallel sides and thickened walls but lacking an elevated flap or ridge. Filaments smooth, white, narrowly oblong to linear and scarcely, if at all, tapering to either apex or base, about 3-5 mm. long and about 0.8-1.0 mm. wide. Connective bluntly rounded, whitish, and extending 0.5-2.0 mm. beyond the anther-sacs. Anther-sacs bright yellow, about 6-9 mm. long. Ovary conspicuously triquetrous and very indistinctly, if at all, stipitate; tapering from its widest point at the middle to both apex and base; the three sides each slightly concave and at least not noticeably medially grooved, about 3-4 (-5) mm. high and each face about 1.5-2.5 mm. wide. Style united for at least four-fifths of the distance from the ovary to the stigmatic tips which at maturity are widespreading and somewhat reflexed; style and stigmas together about 1.0-1.5 cm. long with the stigmatic lobes about 3.5-5.0 mm. long. Capsule strongly 3-winged, triquetrous and rather abruptly tapering to apex and base so that its rather concave sides appear rhombic in outline, its base sessile and the apex with a conspicuous rostrate beak about 4-7 mm. long and 2 mm. wide; the body of the fruit about 1.5-3.0 cm. long, excluding the beak, and 1.2-2.0 cm. wide. Seed (known only from one imperfect example) globose to subglobose, about 4 mm. in diameter, reddish-brown at maturity with a thickened mound-like ridge or crest extending along either side of the slit-like raphe and perhaps 1/3- (1/2?) encircling the seed. Moist and often poorly drained bottomland hardwood forests along the Coastal Plain from South Carolina into northern Florida and west into Mississippi (Fig. 3).

This little-collected species is known only from the bottomlands and floodplains of the southeastern Coastal Plain. It is readily distinguishable from its nearest relative *U. sessilifolia*, which also possesses sessile leaves and an elongated rhizome, by its long-beaked but sessile fruit and the cordate bract which subtends its flower or fruit.

It seems desirable to cite a specimen of this infrequently collected species from each county in which it is known.

REPRESENTATIVE COLLECTIONS: — SOUTH CAROLINA: BARNWELL CO.: *Batson & Kelley* 30 Mar. 1953 (UNC); BERKELEY CO.: north of Goose Creek Reservoir. *Hunt* 2771 (GA); CALHOUN CO.: 4 miles southeast of Lone Star. *Radford* 9366 (UNC); DORCHESTER CO.: vicinity of Four Holes Swamp. *Ahles* 21906 (UNC). GEORGIA: BURKE CO.: 5 miles west of Waynesboro. *Harper* 2074 (F, GH, MSC, MO, NY, US);

CALHOUN CO.: near Ichawaynochaway Creek, west of Leary. *Thorne & Muenscher 7994* (GA, GH, IA, NY); EARLY CO.: along Odum Creek, west of Blakely. *Thorne & Muenscher 8598* (GA, IA); HOUSTON CO.: between Grovania and Beech Haven. *Harper 1966* (F, GH, MO, MSC, NY, US); LAURENS CO.: Dublin. *Harper 1363* (MO, NY, US); WEBSTER CO.: 2 miles east of Preston. *Thorne & Muenscher 9339* (IA). FLORIDA: — JACKSON CO.: along the Chipola River, between Mariana and Mariana Caverns State Park. *Godfrey 56319* (DUKE, FLAS, FSU, IA, NCSC, NCU, MO, NY, TENN, USF, WVA); LEON CO.: about 6 miles west of Tallahassee. *Godfrey 61910* (DUKE). ALABAMA: MONTGOMERY CO.: wooded bottoms of Catoma Creek. *Harper 83* (GH, MO, NY, US); MISSISSIPPI: OKTIBBEHA CO.: State College. *Eckles 7 April 1937* (MISSA).

3. *Uvularia sessilifolia* L., Sp. Pl. 304. 1753. (Type in Linnean Herbarium. Phototype seen.) *Oakesia sessilifolia* (L.) S. Wats., Proc. Am. Acad. 14: 269. 1879. *Oakesiella sessilifolia* (L.) Small, Fl. Se. U. S. 272. 1903.

Plants completely glabrous but stems and lower surfaces of the leaves glaucous; the stem about (1.7-) 2.5-4.0 (-4.5) dm. high and triquetrous at least above and arising from a branching, whitish, fleshy, subterranean rhizome about 3-5 mm. in diameter. Leaves glabrous, narrowly to broadly elliptic in general outline with a gradually tapering to broadly rounded base and an acute to even short-acuminate apex, mostly (3.7-) 4.5-6.5 (-8.2) cm. long and (1.2-) 1.7-2.7 (-4.0) cm. wide; the leaf subtending the lowest branch mostly about (3.0-) 5.0-7.0 (-7.2) cm. long and (0.8-) 1.0-1.5 (-2.5) cm. wide. Blade-bearing leaves below the lowest branch 1-2. Leaf-margin scarious and very minutely denticulate. Fertile branchlet leafless and hence consisting of no more than the terete peduncle partially fused basally to the leafy axillary stem and about (5.0-) 7.0-14.0 (-18.0) mm. long and one flower. Perianth-segments about (1.2-) 1.5-2.2 (-2.8) cm. long and about 2.0-4.5 mm. wide, gradually tapering to the more or less rounded apex; perfectly smooth both externally and internally, very pale yellow. Tepals narrowing basally into a thickened, somewhat fleshy, channeled base about 1.2-1.8 mm. long with a well-defined, narrow, nectiferous depression about 0.8-1.0 mm. long and about 0.5-0.8 mm. wide with more or less parallel sides and thickened walls but lacking an elevated flap or ridge. Filaments smooth, narrowly oblong to linear and scarcely, if at all, tapering to either apex or base, about (2.0-) 2.5-5.0 (-6.5) mm. long and 0.6-0.8 mm. wide. Connective bluntly rounded just above the anther-sacs and barely, if at all, extended beyond them. Anther-sacs about 5.0-10.0 (-13.0) mm. long. Ovary conspicuously triquetrous and clearly stipitate, tapering from the widest point at the middle to both apex and base; the three sides slightly concave and at least not conspicuously medially grooved, about 3.0-5.0 mm. high excluding the 0.8-1.2 mm. long stipe and each face about 1.5-3 mm. wide. Style united for at least four-fifths of the distance to the stigmatic tips which some-

what reflex in age; style and stigmas together about 1.0-1.5 cm. long and the stigmatic lobes about 1-2 mm. long. Capsule conspicuously three-winged, triquetrous and roundedly tapering to both apex and base; its sides somewhat concave and each face appearing broadly elliptic in outline; its base conspicuously stalked with the stalk usually about 2-4 (-6) mm. long; the fruit about (1.2-) 1.5-2.7 (-3.2) cm. long (excluding the stipe) and (0.8-) 1.0-1.5 (-1.8) cm. wide. Seed globose or nearly so, about 3-4.5 mm. in diameter, reddish-brown at maturity with a thickened mound-like ridge or crest extending along either side of the slit-like raphe which half encircles the seed. Typically found in moist hardwoods and especially in bottomlands but (particularly in the northern midwest) also encountered in more xeric sites including even jack pine woods; ranging from Nova Scotia south into northern Florida and west into North Dakota and Louisiana (Fig. 4).

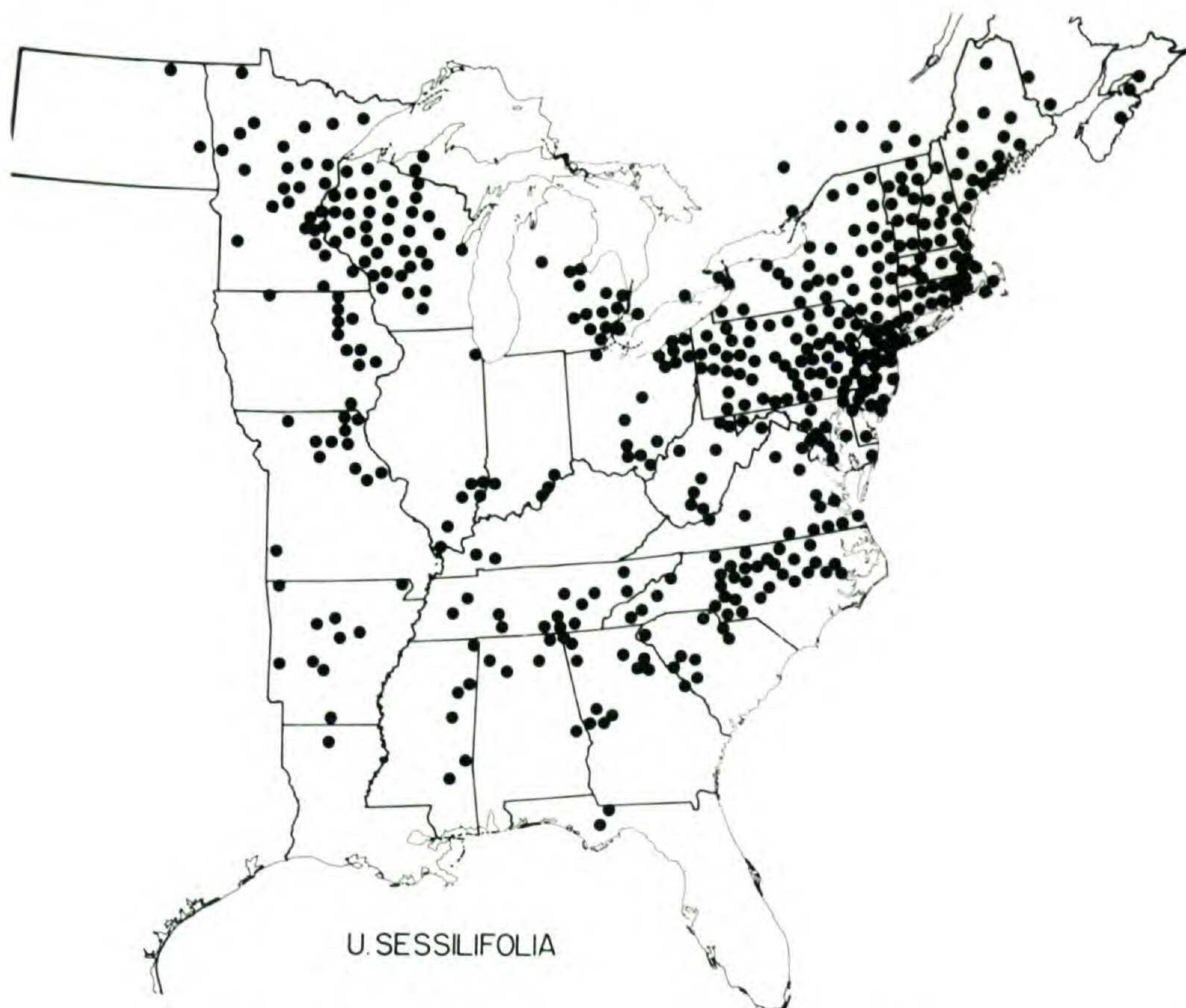


Fig. 4. Distribution of *Uvularia sessilifolia*

4. *Uvularia grandiflora* J.E. Sm., Exot, Bot. 1: 99. t. 51. 1804. (Type not seen. Description and plate seemingly conclusive.) *U. perfoliata* α *major* Michx., Fl. Bor.-Am. 1: 199. 1803. (Type not seen. Description thought to be conclusive.) *U. grandiflora* f. *latifolia* Louis-Marie, La Revue d'Oka 14: 153. 1940. (Type not seen.) *U.*

grandiflora f. *variegata* Louis-Marie, La Revue d'Oka 14: 153. 1940. (Type not seen.)

Plant glabrous except for the lower surface of the leaves; the stem terete and about (2.0-) 4.0-7.0 (-8.0) dm. tall. Leaves sparsely to very densely pubescent beneath (or very rarely glabrous); the trichomes extremely short to rather long, ranging in length from about .05-0.5 mm. long; mostly (4.0-) 7.0-12.0 (-13.5) cm. long and (2.0-) 3.0-5.0 (-5.5) cm. wide, ovate-oblong to somewhat elliptic in general outline with a broadly rounded base and an acute to short-acuminate apex; the leaf subtending the lowest branch mostly about (6.5-) 9.0-12.0 (-13.5) cm. long and (2.0-) 2.5-3.5 (-5.5) cm. wide. Blade-bearing leaves below the lowest branch typically but one. Leaf-margin smooth and very narrowly scariously rimmed. Fertile branchlet bearing one perfoliate leaf and one flower on a peduncle about (1.0-) 1.2-2.0 (-2.5) cm. long. Perianth segments about (2.0-) 2.5-4.5 (-5.0) cm. long and about (2.5-) 3.0-7.0 (-9.0) mm. wide, acute to acuminate, perfectly smooth both externally and internally, pale yellow. Tepals fleshy-thickened at base with a shallow nectariferous depression about 2 mm. long and 1 mm. wide bordered distally by a very slightly elevated ridge or mound about 0.1 mm. high. Filaments smooth, more or less oblong but noticeably tapering towards both base and apex from a point approximately two-fifths the distance from base, about (2.0-) 3.0-6.0 (-7.0) mm. long and 0.5-1.2 (-1.6) mm. wide. Connective extending beyond the anther in an inwardly arching, obtusely conical beak about 0.2-0.7 mm. long and 0.4 mm. wide and not at all indented at apex. Anther-sacs elongate, about (8-) 12-15 (-20) mm. long. Ovary oblong-cylindric in general outline, obtusely and moderately 3-lobed with each segment slightly longitudinally grooved medially, about 2.5-4 mm. high, sessile. Style united for about one-fifth to one-third or rarely two-fifths the distance from the base towards the stigmatic tip; stigmatic tips slightly reflexing with age; style and stigmas together about 9-12 mm. long. Capsule with a rounded to nearly truncate apex and more or less obpyramidal in general outline but moderately 3-lobed and each lobe itself very slightly grooved; mostly about 0.8-1.5 cm. high and (1.0-) 1.2-1.7 (-2.2) cm. wide at its broadest point. Seed nearly globose, but often partially compressed out of shape, about 3-5 mm. in diameter, reddish-brown at maturity, about one-third to one-half enveloped by a thin membranous covering. Rich and usually moist hardwood-forested slopes and bottomlands from southern Quebec south along the mountains into Alabama (and even as far as southern Mississippi) and west into Arkansas, the eastern Dakotas and southern Ontario (Fig. 5).

The possibility that this binomial may be superceded by *U. lanceolata* Ait. is discussed under that binomial with the Doubtful and Excluded Names at the end of this paper.

Dietz (1952) has discussed introgression in both this and the following species under which I have presented a few comments. Most of the specimens that have proved difficult to identify resemble *U. grandiflora* in most particulars except that they are glabrous or very nearly so.

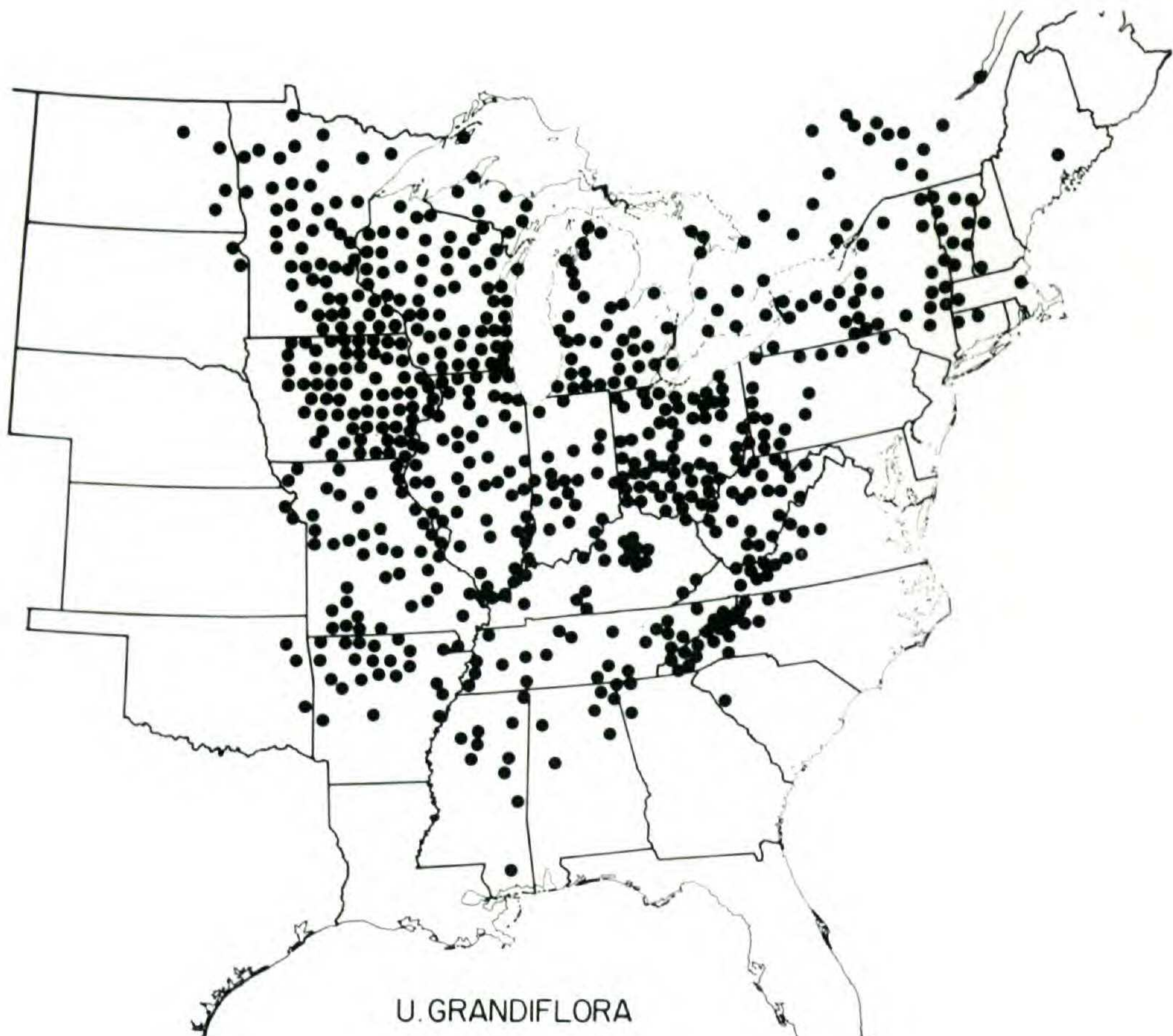


Fig. 5. Distribution of *Uvularia grandiflora*

5. *Uvularia perfoliata* L., Sp. Pl. 304. 1753. (Type in the Linnean Herbarium. Phototype seen.) *U. perfoliata* β *minor* Michx., Fl. Bor.-Am. 1: 199. 1803. (Type at Paris; not seen, description seemingly definite.) *Uvularia flava* J. E. Smith, Exot. Bot. 1: 97. 1804. (Type not seen. Plate and description seemingly adequate for determination.)

Plant completely glabrous; the stem slightly to heavily glaucous and about (1.5-) 2.0-3.5 (-6.0) dm. tall with (1-) 2 very slender, subterranean, slightly geniculate stolons up to 1.5 dm. long (apparently present only early in growing season). Leaves glaucous beneath, mostly

(3-) 4-8 (-12) cm. long and (1.5-) 2-4 (-6) cm. wide, ovate to ovate-oblong in general outline with a broadly rounded base and an acute to abruptly short-acuminate apex; the leaf subtending the first branch mostly about 4-8 (-10) cm. long and 2-5 cm. wide. Blade-bearing leaves below the first branch typically 3-4 but occasionally fewer. Leaf-margin smooth and very narrowly scariously rimmed. Fertile branchlet bearing one perfoliate leaf and one flower on a peduncle about (0.6-) 1.0-1.8 (-2.4) cm. long. Perianth segments (1.5-) 2.0-3.0 (-3.7) cm. long and about 3-5 (-6) mm. wide, acute, densely papillose-tuberculate within, pale yellow but typically of an orange color in the area of the rounded mound-like papillosities; the rounded, half globose to oblong papillose beads varying greatly in size on each tepal, ranging from about 0.2-0.5 (-1.0) mm. long. Tepals fleshy-thickened at base with a shallow but pronounced nectariferous depression about 1.5 mm. long and about 1 mm. wide and with an inconspicuous ridge bordering each side of the nectary. Filaments smooth, more or less oblong but noticeably tapering to both base and apex from a point about one-half the distance from base towards the apex, about 3-4 mm. long and 1.0-1.5 mm. wide, rather turgid. Connective extending beyond the anther into an inwardly arching acute beak about 1 mm. long and about 0.5 mm. wide, very slightly indented at apex. Anther-sacs about 7-10 mm. long. Ovary oblong-cylindrical to obpyriform in general outline, obtusely and deeply 3-lobed with each lobe again slightly indented medially, about 3 mm. high, very slightly elevated at base by receptacular bulge but sessile and not stipitate. Style united for about half to two-thirds the distance to the stigmatic tip; stigmatic tips reflexing with age; style and stigmas together about 8-10 mm. long. Capsule nearly truncate at apex and obpyramidal in general outline but strongly 3-lobed and each lobe itself deeply 2-lobed with the lobes appearing apically rostrate, mostly about 0.8-1.3 cm. high and 1.2-1.6 cm. wide at apex. Seed subglobose to plumply reniform, about 3-6 mm. long, reddish-brown at maturity, one-third to one-half enveloped by a thin membranous, previously balloon-like covering originating from the funiculus and outer integument. Usually in open to densely forested deciduous slopes or well-drained uplands but occasionally in floodplain or swampy forests and more rarely growing in piney woods or even in meadows or along road or railroad embankments; ranging from southern New Hampshire and southern Ontario south into northern Florida and westward into central Ohio and Louisiana (Fig. 6).

Dietz (1952, p. 243) has suggested that *U. flava* J. E. Smith was a hybrid ("probably an introgressive hybrid, or perhaps even an F_1 ") between *U. perfoliata* and *U. grandiflora* stating that it resembled *U. perfoliata* "but with deeper yellow flowers and perianth smooth within — floral characteristics which suggest *U. grandiflora*." Dietz also con-

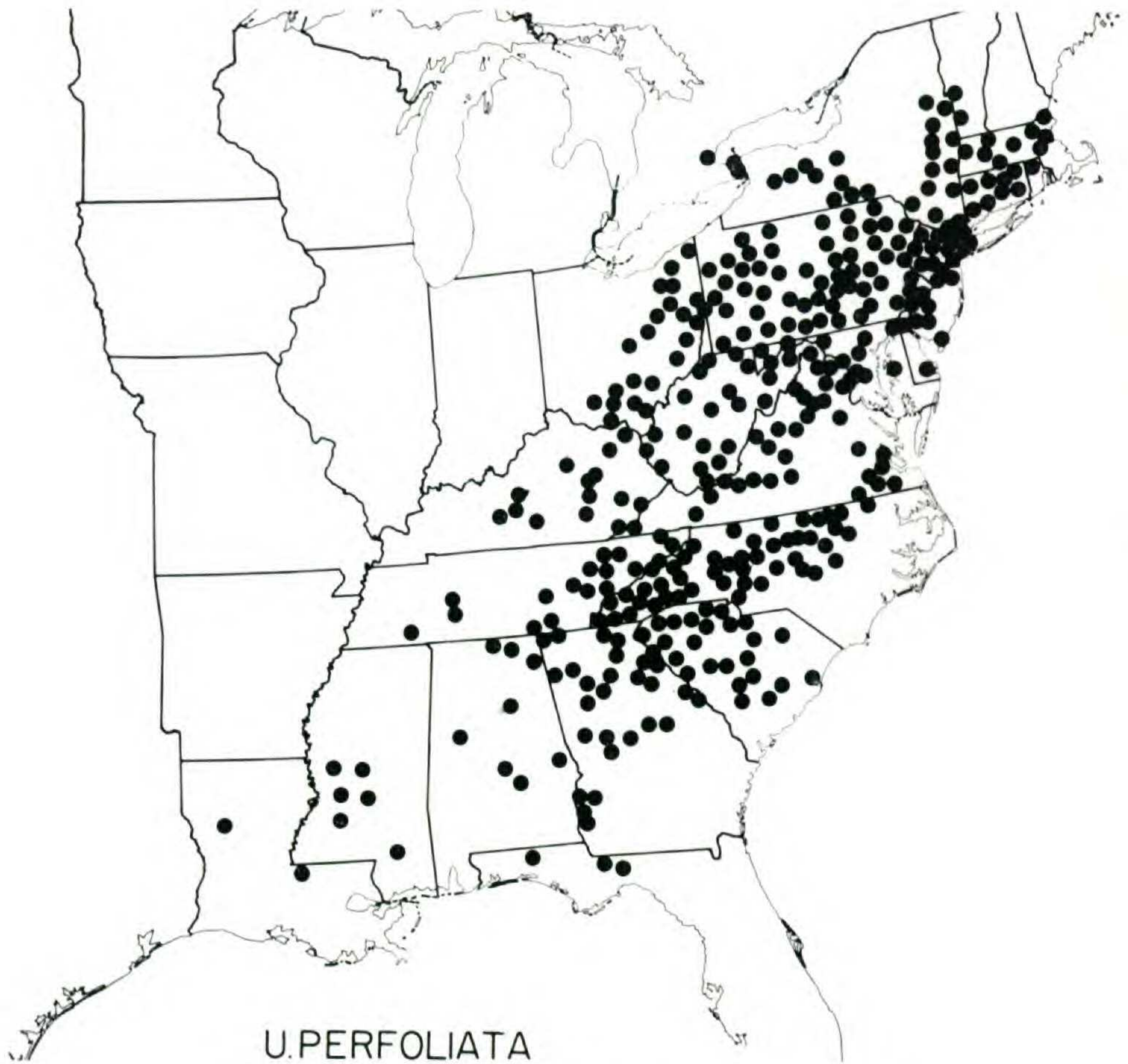


Fig. 6. Distribution of *Uvularia perfoliata*

cluded that "*U. flava* apparently disappeared gradually, for the manuals of the day reflect increasing uncertainty about it until it finally was dropped into synonymy with *U. perfoliata* and was removed entirely from the literature." Smith, however, in both the plate and the original accompanying description clearly indicated that the tepals were tuberculate-roughened within and that the anthers were pointed. He admitted that although he felt *U. flava* to be distinct from *U. perfoliata* "it is very difficult to express a specific distinction." The flower of *U. flava* was described as being "remarkably different, larger, more taper and elongated, with narrower sharper petals, an inch long, yellow, with orange-coloured tubercles on the inside" and the point of the anthers are "also longer and more conspicuous." In contrast the tepals of *U. perfoliata* were described

by Smith to be "scarcely half an inch long, of a very pale greenish buff-colour", and with "their inner side rough with yellowish protuberances." There is no evidence in the original account that would indicate that *U. flava* was anything other than a more orange-tinted race of *U. perfoliata*; there certainly is nothing to indicate that Smith was describing either an F_1 or introgressant between *U. perfoliata* and *U. grandiflora*. Watson (Proc. Am. Acad. 14: 268. 1879) placed *U. flava* in the synonymy of *U. grandiflora*, a disposition which caused Gray (Am. Jour. Sci. ser. 3. 18: 313. 1879) to express surprise.

Anderson (1954) and his student Dietz (1952) have both agreed that much of the variability observed within the perfoliate species of *Uvularia* is the result of introgressive hybridization. Amazingly, Anderson, on the basis of a detailed study of only ten herbarium specimens "selected at random" of each of the two perfoliate species, was able to conclude that 1) the specimens of *U. grandiflora* formed a "coherent group", 2) those of *U. perfoliata* were "not so coherent" and 3) the variation within the last mentioned species was due to introgression from *U. grandiflora*. Dietz's (1952) more lengthy investigation convinced him that *U. grandiflora* was introgressing into *U. perfoliata* and that any introgression of *U. perfoliata* into *U. grandiflora* would be obscured by the possibility of undetected introgression from any of the sessile-leaved taxa. These sessile-leaved species, Dietz felt, were more closely related to *U. perfoliata* than that species was to *U. grandiflora*. In fact Dietz indicated that the sessile-leaved taxa would be somewhat intermediate in morphology and hence apparently in taxonomic position to the two perfoliate species but closer in their affinities to *U. perfoliata*. This conclusion as to relationship is in my opinion highly erroneous and demonstrates aptly the dangers inherent in weighing all characters and even tendencies as of equal importance in what certainly must be judged as a futile effort to achieve objectivity. Science will be advanced further by the more normal taxonomic procedure of attempting to evaluate the significance of the char-

acters and basing classification upon the results of these considered judgments. Only a distorted picture can be expected if one treats rather ill-defined tendencies such as the number of fruit per plant and general leafiness as being equally significant in determining relationships as the unvarying characters with strong morphologic bases such as the nature of the underground parts, the manner of attachment of the medial cauline leaves, fruit shape, presence or absence of ornamentation upon the tepals and the very different raphial outgrowths of the seeds.

Anderson and Whitaker (1934) point out that taxonomists tend to "think of species in terms of the precise differences which permit their ready classification" and that "to them the really essential differences between *U. grandiflora* and *U. perfoliata* will be those few discontinuous ones which are ordinarily used in identifying the species." Anderson and Whitaker contrasted this taxonomic viewpoint with that of those whose interest was "in the biological makeup of the units which are being classified" and stated this latter group found that "the many slight overlapping differences between species are more characteristic than the few sharply discontinuous ones." A taxonomist can be expected to be biased towards the advantages of the outlook held by his own discipline and my own study of *Uvularia* certainly did not present evidence that would convince me of the validity of this so-called "biological" viewpoint.

It seems reasonable to conclude that the "variants more or less difficult to classify" found in the area of overlap between the ranges of the two perfoliate species might well be the result of introgression between those two species and my experience with the genus emphatically confirms Dietz's conclusion "of the relative rarity of introgression as a factor in the perfoliate *Uvularias*." The most useful character in distinguishing the two perfoliate species is the presence or absence of papillae upon the inner surface of the tepals. No specimen possessing tepals proved to be a problem in identification; those lacking them occasionally did. Dietz's study was based upon mature specimens which, of course,

lack tepals. A taxonomist attempts to identify specimens in all stages of maturity but he would consider it a pointless handicap not to utilize those characters which experience has shown to be the most reliable and instead to insist upon basing the study upon specimens in those stages most difficult to distinguish.

Anderson (1953) attempted to refute those who have felt that at least part of the variability encountered within species or even variability shared between segments of two supposedly distinct taxa might be due to common ancestry (i. e., a common "store of variability" or the "genetic pool hypothesis"). It still would appear that those features, thought by Anderson or Dietz to be indications of introgression, such as the number of fruit borne on each plant, general leafiness, position of the longest internode, ratio of leaf-width to leaf-length, are all variable to the degree of overlapping between the two species. The noted variation is hence not necessarily the result of hybridization. Actually, Dietz admits the possibility of plants of "good" *U. perfoliata* with more than one fruit and leaves more numerous than nine but in spite of this both of these features are used as evidence of introgression from *U. grandiflora* when coupled with longer internodes and a higher ratio of leaf width to length since "where introgression is a factor, there is a strong tendency for the sum of the measured characters to vary together." To one who is not a student of introgression, it would seem only proper to rule out as evidence of introgression those features that normally vary sufficiently in one species to match the condition characteristic of the other species.

Characteristic of Dietz's approach are the comments made about a population of the midwestern perfoliate species from Missouri in which was noted "the complete absence of plants with more than one fruit." This was followed immediately by the statement that *U. sessilifolia*, which is found in Missouri, "is typically a single-fruited plant." A population sample from northern Minnesota "suggests strongly an introgression from *U. sessilifolia*" by the "presence of some

sessile leaves on the upper portions of occasional plants", a more strongly divergent primary branch "as in *U. sessilifolia*" and "the gross appearance of the plant." Suspicion of miscegenation was so great that it was thought to be "noteworthy that a *Uvularia* cross apparently did not occur at Hawley [Pennsylvania] where two species occur together." Throughout most of the generic range two or more species grow either together or more characteristically in close proximity to one another. Evidence of hybridization between any of these species is certainly slight and between most species non-existent. Much of the published "evidence" is indeed flimsy and highly circumstantial and hence is anything but convincing. It would be of the greatest interest to know if it were possible for crosses to occur between species of the two sections recognized in this account of the genus and in spite of the considerable time and effort that might be required to attempt such experimental crosses this would seem to be the only certain way to demonstrate or even to disprove partially the possibility of intersectional crosses. Certainly evidence of the circumstantial sort previously presented cannot be accepted. The judicial Anglo-Saxon precept of "innocent until proven guilty" ought to be extended by botanists to plants. Baker's (Nature 159: 221-223. 1947) recommendation that "wherever possible, artificial crosses between the forms involved . . . should precede investigations of natural populations" has much merit in spite of Dietz's excuse that "experimental data would involve a prohibitively long investigation." These lengthy investigations appear to be the only ones that will provide the desired information.

DOUBTFUL AND EXCLUDED NAMES

- Uvularia acutifolia* Raf., Am. Monthly Mag. 359. 1817. *nom. nud.*
Uvularia amplexicaule Mill., Gard. Dict. ed. 8. No. 1. 1768. = *Streptopus amplexifolius* (L.) DC., Fl. Fr. 3: 174. 1805.
Uvularia amplexifolia L., Sp. Pl. 304. 1753. = *Streptopus amplexifolius* (L.) DC., Fl. Fr. 3: 174. 1805.
Uvularia Betua Buch.-Ham. ex D. Don, Trans. Linn. Soc. 18: 517. 1841. *nom. illegit.* (Art. 34.4). Published in synonymy of *Disporum Hamiltonianum* (Wall.) D. Don, *l.c.*

Uvularia calcarata Wall., Cat. n. 5087. 1831-32. = *Disporum calcaratum* (Wall.) D. Don, Trans. Linn. Soc. 18: 516. 1841.

Uvularia caroliniana (Gmel.- Wilb., Rhodora 63: 39. 1961. (= *Anonymos pudica* Walt., Fl. Car. 123. 1788. *nom. illegit.* Art. 43. *Erythronium carolinianum* Gmel., Syst. Nat. 2(1): 546. 1791. *U. pudica* (Walt.) Fern., Rhodora 41: 536. 1939. *nom. illegit.* Art. 43.)

I now belatedly concur with Dietz's conclusions (1952, p. 226), if not completely with his reasoning, that Walter's account, the basis for all the above-mentioned synonyms, is too uncertain as to the species (or species) described to warrant the abandonment of Michaux's clearly-defined and certain binomial, *U. puberula*. It now would appear that both Fernald and I relied too heavily upon the note made by Asa Gray after examining the specimens in Walter's herbarium in 1839 that "*Anonymos* (Erythronio aff.) *pudica!* = *Uvularia puberula*." Even though Gray may well have seen a specimen of what is here called *U. puberula* in Walter's herbarium, it does not follow that the specimen seen by Gray should be accepted as the type of *Anonymos pudica* in view of the conflicting statements in the original account in Walter's Flora. The fruit and seed were described by Walter in the generic description as follows:

Per. *capsula* turbinato-triangularis, angulis bifidis, trilobularis, trivalvis.

Sem. *bina* in singulo loculamento depresso-globosa, ab uno latere cincta membrana vesiculari.

The distinguishing features mentioned here are "*capsula turbinato-triangularis, angulis bifidis . . .*" and "*. . . ab uno latere cincta membrana vesiculari*". This best describes *U. perfoliata* which possesses an inversely pyramidal capsule deeply lobed at each of the three apical angles and a bladderly membrane half-encompassing the seed. These features certainly exclude from consideration any member of section *Oakesiella*, all of which possess hornless, triquetrous capsules tapering to both apex and base and seeds with a hardened, double ridge extending half-way around each in a manner resembling the crest on a Roman helmet.

In the diagnosis of Walter's species, the only even vaguely delimiting term is "*foliis amplexicaulibus*". Michaux de-

scribed the leaves of *U. puberula* as sub-amplexicaul, and, although any such term seems to be an overemphasis of the sessile leaves of this species, it still would appear to be a better description of it than of the perfoliate leaves of *U. perfoliata*. And of course Gray, as reported by Fernald (*Rhodora* 41: 537. 1939), did identify a specimen that he took to be *Anonymos pudica* as *U. puberula* in Walter's collection.

In view of the certainty of the identity of the plant included in Walter's generic description as being other than the species to which the name has been applied and the inconclusiveness of the one word in the original diagnosis for the species, which might be considered at all diagnostic, it would seem best to treat Gmelin's binomial, based completely as it was upon Walter's account, as a *nomen dubium* and to take up again Michaux's unequivocal *U. puberula*.

Uvularia chinensis Ker-Gawl., Curtis Bot. Mag. t. 916. 1806. = *Disporum cantoniensis* (Lour.) Merr., Phil. Jour. Sci. 15: 229. 1919.

Uvularia cirrhosa Thunb., Fl. Jap. 136. t. 2. 1784. = *Fritillaria*.

Uvularia distorta (Michx.) Pers., Syn. Pl. 1: 360. 1805. = *Streptopus amplexifolius* (L.) DC. var. *americanus* Schultes, Syst. Veg. 7: 311. 1829. (= *Streptopus distortus* Michx., Fl. Bor.-Am. 1: 200. 1803).

It is very doubtful if Persoon actually should be charged with having published this combination for it appears under the genus *Uvularia* merely as "7. *amplexifolia (distorta)*, . . ."

Uvularia grandifolia Pursh, Fl. Am. Sept. 1: 231. 1814. [typographical error for *U. grandiflora* J. E. Sm.]

Uvularia Hamiltoniana Wall., Cat. n. 5088. 1831-32. = *Disporum calcaratum*, (Wall.) D. Don var. *Hamiltonianum* (Wall.) Baker, Jour. Linn. Soc. Bot. 14: 589. 1875.

Uvularia hirta Thunb., Fl. Jap. 136. 1784. = *Tricyrtis hirta* (Thunb.) Hook., Bot. Mag. t. 5355. 1863.

Uvularia lanceolata Soland. in Ait., Hort Kew. 1: 434. 1789. A strong suspicion exists that Solander here for the first time provided a binomial for the plant that is now called *U. grandiflora*.

Aiton's account is presented below in full.

lanceolata. 2. U. foliis perfoliatis ovato-lanceolatis acuminatis.

Polygonatum ramosum flore luteo minus *Corn. canad.*
40. tab. 41.

Spear-leav'd *Uvularia*.

Nat. of North America.

Introd. 1785, by Mr. Archibald Menzies.

Fl. July

H. 4.

Cornut's plate is anything but diagnostic but there is a slight hint of *U. grandiflora* in the leaves depicted as there is also in the diagnostic phrase of Aiton and the suggested common name. Pursh (Fl. Am. Sept. 1: 231. 1814) equated Aiton's name to *U. grandiflora* "according to specimens in the Herbarium of A. B. Lambert, Esq." while Baker (Jour. Linn. Soc. Bot. Lond. 17: 462. 1879) includes *U. lanceolata* in the synonymy of *U. perfoliata* noting that it "est forma mera angustifolia". The name obviously should remain unassigned until authentic specimens are discovered.

- Uvularia lanuginosa* (Michx.) Pers., Syn. Pl. 1: 360. 1805. = *Disporum lanuginosum* (Michx.) Nicholson, Dict. Gard. 2: 485. 1884.
- Uvularia lanuginosa* β *major* Hook., Fl. Bor.-Am. 2: 174. 1838. = *Disporum trachycarpum* (S. Wats.) Benth. & Hook. f., Gen. Pl. 3: 832. 1883.
- Uvularia Leschenaultiana* Wall., Cat. n. 5089. 1831-32. = *Disporum Leschenaultianum* (Wall.) D. Don, Trans. Linn. Soc. 18: 518. 1841.
- Uvularia multiflora* Reinw. ex Kunth, Enum, Pl. 4: 207. 1843. *nom. illegit.* (Art. 34.4). Published by Kunth in the synonymy of *Disporum multiflorum* Don, *l.c.*
- Uvularia oppositifolia* Schlecht. ex Kunth, Enum. Pl. 4: 254. 1843. *nom. illegit.* (Art. 34.4). Published by Kunth in the synonymy of *Fritillaria camtschaticensis* (L.) Ker., Bot. Mag. sub t. 1216. 1809.
- Uvularia parviflora* Wall., Asiatic Res. 13: 378. 1820. = *Disporum parviflorum* (Wall.) D. Don, Prodr. Nep. 50. 1825.
- Uvularia Pitsutu* Buch.-Ham. ex D. Don, Prodr. Fl. Nep. 50. 1825. *nom. illegit.* (Art. 34.4). Published by Don in the synonymy of *Disporum Pitsutu* Buch.-Ham. ex D. Don, *l.c.*, = *Disporum cantoniensis* (Lour.) Merr., Phil. Jour. Sci. 15: 229. 1919.
- Uvularia puberula* J. E. Sm., Rees. Cycl. 37: No. 5. 1818. = *Disporum Smithii* (Hook.) Piper, Contr. U. S. Nat. Herb. 11: 201. 1906.
- Uvularia pudica* (Walt.) Fern., *nom. illegit.* see discussion under *U. caroliniana*.
- Uvularia rosea* (Michx.) Pers., Syn. Pl. 1: 360. 1805. = *Streptopus roseus* Michx., Fl. Bor.-Am. 1: 201. 1803.
- Uvularia sessiliflora* J. F. Gmel. Syst. Nat. ed. 13.2: 1642. 1792.
- Uvularia sessilis* Thunb., Fl. Jap. 135. 1748. = *Disporum*. The combination *D. sessile* has been attributed to D. Don (Fl. Nep. 50. 1825) but it was not made there according to the strictures of Art. 33. The only reference there by Don is made following the generic description and is as follows: "Obs. Huc *Uvularia chinensis* Bot. Mag. et *Uvularia sessilis* Thunb. Jap. cui folia, sessilia, et flores subsolitarii albi." But since Thunberg included the binomial *U. sessilifolia* L. as a synonym, it would appear that the legitimacy of the name itself ought to be investigated thoroughly.
- Uvularia Smithii* Hook., Fl. Bor. Am. 2: 174. t. 189. 1838. = *Disporum Smithii* (Hook.) Piper, Contr. U. S. Nat. Herb. 11: 201. 1906.

- Uvularia umbellata* Wall., Asiatic Res. 13: 379. 1820. = *Disporum cantoniensis* (Lour.) Merr., Phil. Jour. Sci. 15: 229. 1919.
Uvularia ? viridescens Maxim., Prim. Fl. Amur. 273. 1859. = *Disporum smilacinum* A. Gray, Perry Jap. Exped. 2: 321. 1856.

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REFERENCES CITED

- ANDERSON, E. 1953. Introgressive hybridization. Biol. Rev. 28: 280-307.
———. 1954. Efficient and inefficient methods of measuring specific differences. pp. 93-106 in O. Kempthorne *et al.* Statistics and mathematics in biology. Iowa State College Press, Ames.
———. AND T. W. WHITAKER. 1934. Speciation in *Uvularia*. Jour. Arnold Arb. 15: 28-42.
DIETZ, R. A. 1952. Variation in the perfoliate *Uvularias*. Ann. Missouri Bot. Gard. 39: 219-247.
SMALL, J. K. 1903. Flora of the southeastern United States. (*Uvularia* and *Oakesiella* pp. 268, 271 & 272, 1328). Lancaster, Pa.
———. 1933. Manual of the southeastern flora. (*Uvularia* and *Oakesiella* pp. 295, 299 & 300, 1500.) New York.
WATSON, S. 1879. A revision of the North American Liliaceae. Proc. Am. Acad. 14: 213-288.